a region that included the NP95 plant homeodomain (PHD) region (Figure 1). It is interesting that, in their assay, they also observe NP95 binding to part of the DNMT1 carboxy-terminal methyltransferase domain, although it is unclear whether this interaction is mediated through the NP95 PHD domain or another domain. NP95 (under various names) had been previously identified as a protein involved in cell-cycle progression, sensitivity to genotoxins, and DNA replication, and it remains to be seen whether these effects are related to changes in genomic methylation patterns or reflect some other function of NP95.

NP95 adds to a growing list of factors that have been genetically determined to be involved in the establishment or maintenance of genomic methylation in mammals but are not DNA methyltransferases. Cells or mouse embryos deficient in DNMT3L, MILI, MIWI2, CGBP, Lsh or both Suv39h1 and Suv39h2 all display some degree of demethylation in one or more sequence compartments. With the exception of DNMT3L, which has been shown to be involved in establishment of genomic methylation patterns, it remains unclear whether these other factors play roles in establishment and/or maintenance, and the mechanisms through which they function remain to be determined. These new studies on NP95 not only represent the identification of a factor involved in the maintenance of global methylation patterns, but also might reconcile the limited dependence of DNMT1 on hemimethylated substrates with the faithful mitotic inheritance of genomic methylation patterns.

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Active Sensing: Matching Motor and Sensory Space

A recent study has shown that, unusually, both the sensory and motor capabilities of an electric fish are omnidirectional. This matching of motor and sensory spaces helps the fish to hunt prey efficiently — particularly important given their energetically costly active sensory system.

Stefan Schuster

Bats, electric fish and head-shaking locusts have one thing in common: they all invest energy into probing actions that help them to obtain useful information about their surroundings from sensory feedback. In some animals, the energy invested in such 'active sensing' can be substantial, so that best possible use should be made of the investment. A recent study shows how this is done in hunting electric fish that use a particularly costly active sensory system. Using a combined behavioral and computational approach, Snyder *et al.* [1] were able to determine the precise shapes of the volume of surrounding space a hunting electric fish can probe for the presence of its prey and of the motor space in which the fish can actually maneuver to make a catch.

The black ghost knifefish (*Apteronotus albifrons*) studied by Snyder *et al.* [1] is an amazing creature. It can move elegantly in a wide variety of body orientations and can rapidly switch from one mode of moving to another. Its major propulsion system is its ventral ribbon fin, which runs over almost the full body [1–3]. To probe its nocturnal environment, the fish sends a current across its skin which continuously oscillates at about 1000 cycles per second. With a large number of electroreceptors, tuned to this high frequency [4], the fish monitors how the self-generated current spreads over the fish's surface.

From the way close objects change this distribution, the fish can obtain an electric image of its surroundings. But this way of sensing is costly. At the voltages the fish is able to produce, even close objects cause only minute effects and sensing is restricted to a few centimeters. To increase the range to a mere twelve centimeters, less than the length of the experimental fish, a black ghost knifefish would have to raise its investment from one percent to twice its basal metabolic rate [1].

Snyder *et al.* [1] worked out the volumes within which this fish can sense and reach small *Daphnia* prey in the dark. The three-dimensional sensory space was determined as the set of points in which a moving fish could detect prey with an error rate of less than ten percent. The authors were able to analyse this in detail by using a behaviorally tested, remarkably simple computational model in which the presence of prey was decided from the summed output of all electroreceptors the fish can recruit for the task. The 'motor space' within reach for a cruising fish was quantified from videorecordings of actual prey catching events [1,2], allowing the authors to determine both the range needed for the fish to come to a stop and the ranges the fish could cover within a given time.

This analysis yielded several surprises. For most hunting animals, the places they can reach to make the catch are probably in front of them. Not so in the black ghost knifefish, whose 'motor volume' is omnidirectional. This fish can efficiently reach points in all directions — in dorsoventral direction, to the fish's side and even against its initial heading direction. The sensory volume of this fish is also omnidirectional, and matched in size and shape to the fish's motor volume. Not only does the fish 'illuminate' just that amount of space within which it can harvest prey, but it also matches the shape of the sensory space to its motor capabilities, extending its sensitivity so that it detects a *Daphnia* located at its sides, top or bottom equally well as one located right in front of its mouth.

Black ghost knifefish cruise in their longitudinal direction with a speed that makes their slower waterflea prey float by in a roughly antiparallel direction. If a fish were to invest its energy for sensing as many fleas as it can, it would probably shape its sensory volume into a disk that extends far out from the fish's length axis (Figure 1A). But it would be hard for the fish to profit from this sensory volume: most fleas would have left the thin detection volume before the fish's motor can even be started to change its course. Making things easy for the motor and condensing the sensory volume into a narrow search coil in the fish's longitudinal direction (Figure 1B) would also be better for the fleas than for the fish. While now death is certain for the fleas contained in the narrow sensory volume, all others will pass undetected. Snyder *et al.* [1] show us nicely how sensory and motor capabilities act together to yield a large detection cross-section that the fish is actually able to exploit (Figure 1C).

The sensory and motor volumes of the black ghost knifefish are kept matched even when an increase in water conductivity diminishes the range over which electrolocation works [1]. Much as car drivers must reduce their driving speed when fog cuts sighting distances, hunting black ghost knifefish reduce their cruising speed to keep their motor volumes matched to a smaller sensory volume. Assuming fixed braking power and response latency, the stopping distance of a car would roughly scale with the square of its initial speed. When the sighting range is cut in half, stopping distance should also be halved, which requires a speed reduction by a factor $2^{-1/2}$. This is remarkably close to the actual speed reduction found in the fish.

The computational model of Snyder *et al.* [1] opens up wonderful opportunities to dissect the key factors that act together to shape the sensory and motor volumes. How is omnidirectional sensing achieved despite the concentration of electroreceptors on the head? How could the sensory space be modulated when a strong water current makes the fish's motor space asymmetrical? There is a lot of interest at the moment in active sensing in a variety of systems. Flies, for instance, have to infer their distance from surrounding objects by moving and analyzing the resulting image-motion on their eyes [5,6]. Lindemann *et al.* [7] recently showed that the circuitry blowflies use to do this is tightly matched to the active saccadic 'gaze and fly' strategy used by the flies: only when challenged with image motion that results from the particular way the fly moves does the circuitry work robustly and with no adaptation.

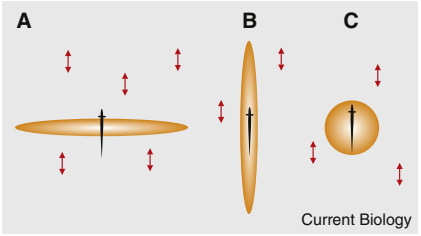

Figure 1. Shaping sensory volumes.
With a given investment of energy into its electric field a swimming black ghost can probe a certain volume of its nocturnal environment for the presence of waterfleas. How should that volume be shaped? (A–C) Three alternatives (top views) which are discussed in the text. Arrows indicate the relative motion of fleas passing a fish that either moves in its forward or backward direction.

Remarkably, an important aspect of the innate relation between sensing and moving was predicted long ago by the mathematician Henri Poincaré [8]. He posed the question of how an animal could arrive at a consistent concept of space and concluded that, without an ability to correlate activity of its effectors with that of its sensors it would have no way of deciding whether sensory changes occur because objects are changing or because they are moving (unchanged) in 'space'. Space is one of the most basic concepts we have about the world, and completely rests on the ability of our nervous systems to link motors and sensors. The new computational tools and virtual reality methods in freely moving animals we now have available will certainly provide further surprises on this intimate relationship.

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